CASTLE — HEREDITY OF HAIR-LENGTH IN GUINEA-PIGS AND ITS BEARING ON THE THEORY OF PURE GAMETES

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# 6. The Origin of a Polydactylous Race of Guinea-Pigs

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# 5. HEREDITY OF HAIR-LENGTH IN GUINEA-PIGS, AND ITS BEARING ON THE THEORY OF PURE GAMETES.

By W. E. Castle and Alexander Forbes.

## 1. INTRODUCTION.

In earlier papers (Castle, :03, :05) it has been shown by one of us that long or "Angora" coat in guinea-pigs and rabbits is alternative in heredity to normal or short coat. It has been shown further that in cross-breeding normal or short coat dominates over long coat, in conformity with Mendel's law of heredity, but that the purity of the gametes formed by cross-breds is not absolute. Impurity of the gametes is indicated by two facts: First, the number of long-haired young produced by cross-bred parents is in excess of the Mendelian proportion, one-fourth; secondly, many of these long-haired young show an imperfect development of the long-haired character, as compared with their long-haired ancestors. Both these facts may be explained by supposing that the alternative characters, short and long hair, which are present in the cross-breds—one seen, the other unseen—have in many cases failed to segregate, or have segregated only imperfectly, when gametes have been produced by the cross-breds. Accordingly the conformity with Mendel's law is a qualified one.

More extended and detailed studies made by us during the past year confirm these conclusions and add several new facts concerning the behavior in heredity of these alternative characters. The idea advanced tentatively by Castle ( :05), that the hair-lengths of guinea-pigs form a discontinuous series of two, three, four or more times the length of short or normal hair, is found to be incorrect. Careful examination of the hair of several hundred guinea-pigs (mostly cross-breds) shows that there occur hairs of practically all lengths from 3.3 cm. up to about 23 cm. The series of supposed maximal hair-lengths of twice 4 cm., thrice 4 cm., etc., resulted from an insufficient number of observations.

## 2. CHARACTER OF FOLLICLE ACTIVITY IN THE PRODUCTION OF SHORT AND OF LONG HAIR.

If an examination is made of the longest hairs plucked from the back of an adult short-haired guinea-pig, it is found that the hairs narrow toward the base, owing to a diminution in the diameter of the medulla, which is entirely wanting in the follicle (see Fig. 1, *A*). Such a hair has ceased to grow, having completed a definite growth cycle, and will sooner or later be shed. This growth cycle was nearing its end when the follicle ceased to form medullary substance. In ordinary guinea-pigs the hair stops growing when it has reached a length of about 4 cm. In long-haired guinea-pigs the hair-follicle does not cease forming medullary substance when a definite hair-length has been attained. The growth of the hair is indefinite, ending only with the degeneration of the follicle itself. The time when this occurs is determined to some extent by the physical condition of the animal. The lifetime of a hair-follicle of this sort may be prolonged by good care, as fanciers well know. Pregnant or nursing mother guinea-pigs frequently lose their longest hair. Insufficient or improper food is likely to have a similar result in either sex. Accordingly, the fancier gives careful attention to the diet of long-haired animals intended for exhibition, and often protects the hair in special ways from mechanical injury. There is, however, no reason to suppose that such care *induces* indefinite activity of the hair-follicle. On the contrary, animals of a short-haired race, under the best of care, will form only hairs of determinate length, whereas animals of a long-haired race, however much abused, will, so long as they live, continue to form hairs of indeterminate growth. The two types of hair-growth are quite distinct, and are sharply alternative in heredity. They are probably paralleled in our own head- and body-hairs respectively, the former being of indeterminate, the latter of determinate growth.

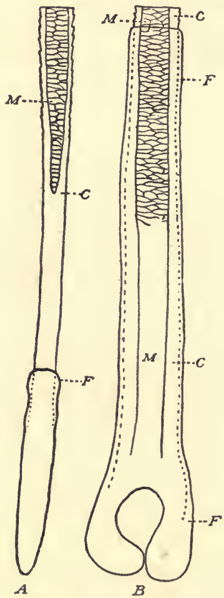


FIG. 1.—*A*, Base of hair, fully grown, of determinate growth type.
*B*, Base of hair of indeterminate growth. From camera drawings, same magnification.
*C*, Cortex; *F*, follicle; *M*, medulla.

Like ourselves, long-haired guinea-pigs bear hairs of both sorts, whereas short-haired guinea-pigs, like our probable simian ancestors, bear only hairs of determinate growth. Similar alternative conditions of hair-growth occur in many different kinds of mammals, as for example in rabbits, goats, cats and horses, the indefinite growth in the latter case occurring in the hairs of the mane and tail only (see Davenport, :04). The long-haired (or indefinite growth) condition is doubtless cœnogenetic in all cases, and has probably arisen independently in each case as a discontinuous variation or mutation. By selection the long-haired condition is easily made a racial character, for long-haired animals produce only long-haired offspring. But without selection, what would be the fate of this mutation? This our breeding experiments may perhaps indicate.

Let us consider first the extreme conditions of follicle activity which we have encountered in the guinea-pigs studied. In long-haired guinea-pigs the hairs all over the body attain a greater length than in short-haired ones, but only hairs of the back and sides grow indefinitely. Accordingly, in comparative studies of the hair-length, it has been found convenient to select a few of the longest hairs to be found on the back or rump of the animal and to use these as a standard of comparison. Following this method the hair of guinea-pigs of different races has been measured at frequent intervals from birth to an age at which the hair had attained full growth.

A litter of four guinea-pigs of a pure short-haired race yielded measurements which combined are expressed graphically in Fig. 2, *A*. Starting at birth with a length of about 18 mm., the hairs grew very rapidly during the first week, at the end of which they measured about 25 mm., an average increase of a millimeter a day; in the second and third weeks they grew less rapidly, measuring about 29 mm. at the end of two weeks, and 33 mm. at the end of three weeks. At this time the growth of the hairs which the animals bore at birth was practically complete; the hair-follicles now ceased to form medullary substance, and consequently the hair narrowed to a base of solid cortex (Fig. 1). From this time on the measurements show from week to week only slight deviations from a length of 33 to 35 mm.

Several series of measurements of the hair of long-haired guinea-pigs, when combined and expressed graphically, are shown in *D*, Fig. 2. The hair-length at birth is about the same as in animals of class *A*, or even a little shorter, but the growth rate does not show the series of rapid changes seen in class *A*. Growth progresses very steadily at an average rate of about 0.83 mm. a day during the first one hundred days and at about 0.75 mm. a day during the second one hundred days. But a glance at Fig. 2, *D*, shows that the slowing up of the growth rate is a very gradual process.

After the hairs have attained a length of about 170 mm. they begin to fall out, but without previously narrowing to a base, as in class *A*. Rarely does a

hair attain a length of 200 mm. As the longest hairs are shed, new ones are found to be growing up to take their places, but there is usually a period, after shedding sets in and before the second-growth hairs are fully developed, when the maximum coat length shows a decided falling off. This is indicated in *D,* Fig. 2, as occurring at about the age of two hundred and and fifty days. The type of hair growth found in class *D* may be called *indeterminate* or continuous; that of class *A, determinate.*

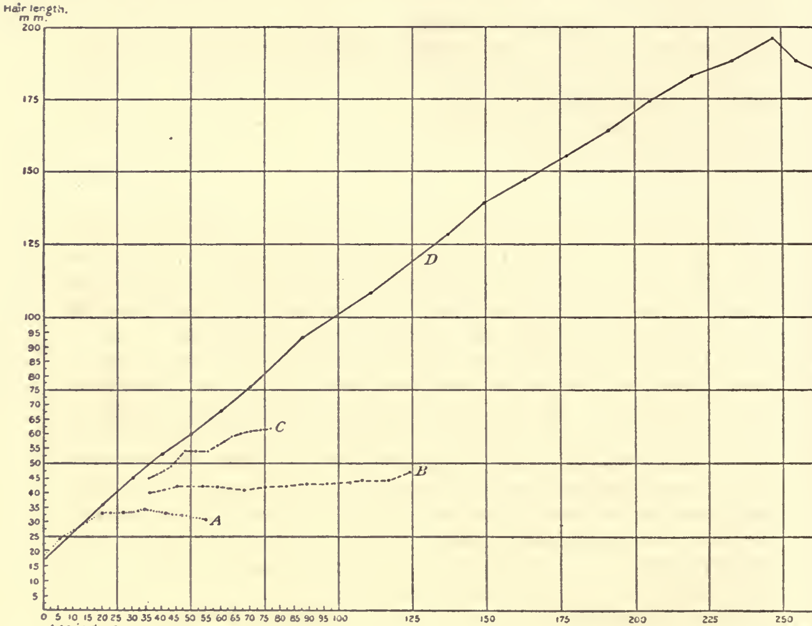


FIG. 2.

Our original stock of short-haired guinea-pigs showed considerable variation in maximal hair-lengths, ranging from 35 to 50 mm., but all of the determinate type of growth (classes *A* and *B,* Fig. 2). The great majority of them would probably have fallen in class *B,* but we can not be sure of this, as many of the animals were no longer available for record when we began making hair-measurements systematically. The hair-lengths recorded for class *A* are certainly exceptionally short, even for animals of determinate hair growth.

### 3. THE EFFECTS OF CROSS-BREEDING BETWEEN SHORT-HAIRED AND LONG-HAIRED ANIMALS.

#### (*a*) MATING $B \times D$.

When the short-haired animals were mated with animals of class *D*, only young of the former sort were obtained, which result shows clearly the dominant character of short hair. However, the maximal hair-length of the cross-breds was usually 40 to 50 mm. (class *B*, Fig. 2); that is, it fell within the *upper* half of the range of variation of the pure short-haired stock, though in no case, we think, did it transcend the range of variation of the short-haired stock itself. We are warranted, then, in concluding that the dominance in the offspring of the short-haired type of growth is complete. Type *B* mated with type *D* gives only type *B*.

#### (*b*) MATING $B(D) \times B(D)$.

But when cross-breds between the types *B* and *D* were bred together, not only did type *D* reappear after skipping a generation, but a new and intermediate type was found also, which we may call type *C*. This is not sharply separated from types *B* and *D*, but is made up of individuals scattered all the way between those parental types. It contained, first, individuals whose hair grew continuously from the age of twenty days on, but much more slowly than does the hair of class *D*, with a tendency to break off at lengths much less than those attained in class *D*. The long hairs of such animals were also frequently less numerous than in typical class *D*, as if *part* of the hairs only were continuous in growth, while the others were determinate. In these individuals we see the alternative characters coexisting as in a mosaic. In other cases animals placed in class *C* appeared to have only hair of determinate growth, but growth continued until a length of 60 to 80 mm. had been attained before the hair narrowed to a base. Such animals represent an intimate blend rather than a mosaic of the contrasted types *B* and *D*, yet with a closer approximation to type *B;* but no sharp line could be drawn between the blends and the mosaics, as the two graded into each other and into the two parental types. These intermediates (class *C*) were about as numerous as the animals of type *D*, but only about half as numerous as those of type *B*. Thus, in a particular experiment there were produced twenty-nine *B*, twelve *C* and ten *D* individuals, together with eleven of unknown character, because they died or were disposed of before their hair was fully grown. The grandparents of this lot were the long-haired male, 2002 (Castle, :05, Pl. 1, Fig. 1), and several different short-haired females; the parents were all of class *B*. The Mendelian expectation

from an experiment like the foregoing is that there will be produced three times as many animals of type $B$ as of type $D$, or in a total of fifty-one young (the number whose character was definitely ascertained) thirty-eight $B$ to thirteen $D$. Comparing with these numbers the observed ones (twenty-nine $B$ and ten $D$), we notice that there are fewer individuals than expected in each of the classes $B$ and $D$, from which we may conclude that each has contributed to the formation of the intermediate class $C$. The hypothesis on which the Mendelian expectation rests is this, that each cross-bred animal will form in equal numbers gametes bearing the pure $B$ character and the pure $D$ character respectively. Evidently from this experiment it follows either that some of the expected $B$ and $D$ gametes are not pure, or else that in this generation the result of a union between a $B$ and a $D$ gamete is not the same as in the original cross. In either case we are forced to admit *modification* of gametes from their original pure condition.

In two other families of guinea-pigs, cross-breds mated *inter se* produced a result similar to that already described. The young in these families were classified as nine $B$, five $C$, two $D$ and four undetermined. These cases differ from the foregoing in that, in producing the cross-breds used, *two* crosses with the $B$ race were made to one with the $D$ race, whereas in producing the first mentioned lot of cross-breds the $B$ and $D$ stocks were equally represented in the ancestry. It is perhaps significant that the $D$ young are relatively fewer in these families, though the total is too small to allow one to attach much importance to the proportions observed among the young.

### (*c*) Mating $B(D) \times D$.

On the Mendelian hypothesis of pure gametes, this cross should yield classes $B$ and $D$ in equal numbers. In matings in which three different $D$ males were employed, it has produced fourteen $B$, seventeen $C$ and nineteen $D$ offspring, together with five of undetermined character. Since $D$ parents are known to form only $D$ gametes, it seems clear from this experiment that the hybrid, or $B(D)$ parent, formed gametes a considerable number of which bore the intermediate or $C$ character. If a single cross of $D$ with $B$ has such an effect in modifying gametes, a repetition of the cross should have a still more marked influence, producing a still larger proportion of intermediate or $C$ gametes. The mating next to be described bears on this question.

### (*d*) Mating $B(D)$ [from Two Successive Crosses with $B$] $\times D$.

Three different $D$ males were used in making this cross. They produced thirty-two $B$, thirty-seven $C$, and twenty-nine $D$ offspring, together with seven of undetermined character. Here the $C$ class is actually larger

than either of the others, though the increase over the last mating is not a very striking one, and several individuals were just on the line between *C* and *D*, so that little stress can be laid upon the classification made.

### (*e*) Mating *B*(*D*) [from Two Successive Crosses with *D*] × *D*.

If two crosses introduce greater contamination of the gametes than one, then the *C* and *D* classes resulting from this cross should be high at the expense of the *B* class. The observed result accords with this interpretation, though the number of young produced is not large. There were one *B*, three *C* and five *D* offspring.

The question now arises, What is the nature of the *C* individuals? Are they the result of partial reversal of dominance, so that when *B* meets *D* in fertilization there is produced an intermediate condition, or have *B* and *D* actually fused to form something different from either? Matings of *C* individuals among themselves or with *B* and with *D* respectively should throw light on this question. If *C* individuals result merely from partial arrest of the dominance of *B*, we shall expect *C* to split at gamete formation into *B* and *D*. If it does not do this we may conclude that it represents a firm union of *B* and *D* to form a new character, *C*.

### (*f*) Mating *C*(*D*?) × *D*.

This mating produced a mixture of *C*'s and *D*'s, in all eight *C*, nine *D* and five individuals of undetermined character. Apparently the *C*'s used in this experiment were heterozygous, producing some *C* and some *D* gametes. The former, combined with *D* gametes, produced *C* individuals; the latter similarly united produced *D* individuals. The fact that no *B* offspring were produced indicates that the *C* parents did not form *B* gametes. We conclude that the *C* gamete is probably a new creation due to a partial and permanent blend of *B* with *D*.

### (*g*) Mating *C*(*D*) [produced by Two Successive Crosses with *D*] × *D*.

This mating should yield a larger proportion of *D* offspring than the last, if cross-breeding introduces contamination of gametes. The observed result was nine *C*, eighteen *D* and six young of undetermined character, which result supports the hypothesis stated. It should be said that in this mating, as in those previously described, the classification of the offspring was wholly unbiased, as it was in each case made before the animal's pedigree was looked up to see in what group of offspring the individual in question should be placed. It must be borne in mind, however, that the *C* group it not a natural one to be considered a unit-character by itself. It

is simply a poorly developed *D*, *C* and *D* being grades, arbitrarily fixed, of the continuous growth type of hair. Or, if we think of *C* as a synthesis of *B* with *D*, then this *C* partakes more largely of the character of *D* the more often the parental *B* has been crossed with *D* in its production. From the fact that the *C* parents give off gametes partaking in different degrees of the *D* character, it seems probable that the synthesis of *B* and *D* to form *C* has been as yet imperfect, as of two ingredients incompletely mixed together, so that different samples contain different proportions of the *D* character. This view is supported by the result obtained by mating *C* with *C*, but as the parents used in this experiment were of different origin from those mentioned in the foregoing pages, it may be well first to describe the source from which they came.

### 4. ORIGIN OF RACE C′, AND RESULTS OF CROSSES IN WHICH IT WAS EMPLOYED.

A family of short-haired guinea-pigs (class *B*), when inbred, produced a few individuals with hair about twice as long as that of their parents. The long hairs were not very numerous. It seems probable, in the light of subsequent studies, that only a few of them were continuous in growth, the others being determinate, but attaining a greater length than do ordinary hairs before growth ceased. When two of these long-haired animals were mated together, all the offspring were long-haired, though some of them had more numerous long hairs than others, or hairs of a greater maximum length. By selecting the best long-haired individuals for two generations a race of imperfectly long-haired individuals was produced, of about the same degree of excellence as the group *C* already described, which was produced by cross-breeding between *B* and *D*. To distinguish it from the latter, we may call this race *C′*.

The *C′* race, bred by itself, produced no *B* individuals, though the maximal hair lengths obtained varied considerably. This result shows clearly that no *B* gametes were produced by the *C′* race, though it had just arisen from the *B* race, in which very likely it had previously been present as a recessive character.

A mating between *C′* and *D* gave a mixture of *C* and of *D* individuals, the two classes being about equally numerous (seven *C* to five *D* in one set of experiments). Certain individuals, however, were just on the line between the two classes, so that no great importance can be attached to the proportions observed. But the result does show, what breeding *C* or *C′* individuals *inter se* had shown, a considerable degree of variability among the *C* and *C′* gametes, this variability being a sufficient basis for selection for increased hair-length. While, accordingly, the variation made its appearance as a discontinuous one, it showed itself amenable to selection.

**5. GAMETES OF CROSS-BREDS OFTEN IMPURE.**

From the foregoing observations it is clear that, while the long-haired and short-haired conditions are sharply alternative to each other in heredity, the gametes formed by cross-breds are not in all cases pure. Frequently they consist of a blend or a mixture of the two alternative conditions, constituting in effect a new condition intermediate between the other two. A study of other characters alternative in heredity yields results somewhat similar.

Albinism is, in heredity, the most sharply alternative of characters, yet cross-breeding between albino and pigmented guinea-pigs may modify the character both of the albino race and of the pigmented one. This modification may take on a variety of forms, as has elsewhere been pointed out (Castle, :05). It may result in the production of mosaics (pigmented animals spotted with white), or of albinos with a modified peripheral pigmentation, or of albinos visibly like their ancestors but transmitting a different set of latent characters. Again, the rough or rosetted coat of certain races of guinea-pigs is sharply alternative to smooth coat, yet cross-breeding of rough with smooth races may induce curious modifications of the rough character or produce smooth individuals bearing the merest trace of the rough character.

All these facts are in harmony with the hypothesis, for which there is strong evidence on the cytological side, that each separately heritable character is represented by a different structural element in the germ (egg or spermatozoon). In fertilization the paternal and maternal representatives of a character become more or less closely united, this union persisting through all subsequent cell-generations until the new individual forms its sexual elements. At that time the paternal and maternal representatives of a character separate from each other and pass into different cells.

But the paternal and maternal representatives of a character may in the meantime have exercised on each other a considerable influence. In the case of some characters, as ear-length in rabbits (Castle, :05[a]), they completely blend and intermingle, so that a new character is produced strictly intermediate between the conditions found in the respective parents.

In other cases the modification may be slight, as if the paternal and maternal representatives of a character had been scarcely more than approximated. Sometimes in cases of alternative inheritance no influence of the cross is observable in certain of the " extracted " individuals, but if any considerable number of individuals is examined, others will be found in which the cross-breeding manifests its influence. From this we conclude that gametic purity is not absolute, even in sharply alternative inheritance.

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